XXVII. *The inheritance of small variations in the pattern of* Papilio dardanus, *Brown.* By G. D. Hale Carpenter, D.M., Oxon.

[Read November 5th, 1913.]

Plates XXXIX and XL.

The work of which this paper is an account was undertaken, at the suggestion of Prof. Poulton, in regard to my family of *P. dardanus* bred from ova laid by a parent of the form *planemoides*, Trim., and exhibited at the meeting of this society on June 4, 1913 (Proceedings, pp. liii–lvi). The resulting female offspring—3 *planemoides* and 7 *hippocoön*, F. (Plate XXXIX), suggested very strongly that the influence of the pattern of the parent is communicated to the pattern of the offspring of a different type. In order to prove this, careful measurements were made of the large divided white spot in the cell of the fore-wing of the 7 *hippocoön* forms, which was in most cases sharply marked and easy to measure. This spot is represented in the *planemoides* form by an orange area in the corresponding position, which at its outer end is not sharply marked, but continuous with the broad orange area forming the band across the fore-wing (Plate XXXIX, figs. 1, 4, 6). In fig. 8 it is seen that part of the orange area in the cell has become separated off, as in *hippocoön*. The spot was measured from the middle of its base at the costa to the extreme tip (often placed on a detached portion), along its longitudinal axis which, if prolonged, leads to the base of a nervure.

[The origin of vein 5 (radial 2) is nearest to the point where the prolonged axis of the spot cuts the end of the cell, and there is little doubt that this is the vein to which the author measured. The marking is often more highly developed on the under surface, and it is there seen that the prolonged spot abuts against the lower or inner marginal half of the middle disco-cellular.—E. B. P.]

Inasmuch as the actual size of the spot will vary, *absolutely*, because of the different size of the individual butterflies, it is necessary to have a common standard by which a small

butterfly can be compared with a larger one. This standard was obtained by expressing the length of the spot as a fraction of the distance from the base of the spot to the base of the nervure [vein 5] along the same axis. The resulting figures are given in percentages; and the different values express the relation between one specimen and another. In one case (Plate XXXIX, fig. 9), the percentage was 102, the spot being so large that its apex extended beyond the cell. The measurements of the spots on *both* fore-wings were taken, and the *average* used for the calculation, as it was found that there were often slight differences between the two sides. By the use of needle-pointed adjustable "dividers" it was found quite practicable to get as near as 0·25 of a millimetre.

It at once became obvious on comparing measurements of the *hippocoön* offspring (Plate XXXIX) derived from *planemoides* with 6 other broods (A–F) of *hippocoön* bred by Mr. W. A. Lamborn near Lagos, W. Africa, from *hippocoön* parents (see A, D, and E on Plate XL), that in the former brood the spot is uniformly large, and that in the latter the specimens are grouped together round a certain average size, which is never so large as the average in the 7 offspring of *planemoides*, and varies for each family. (See *Chart* on p. 663.)

This grouping is very well shown indeed in Brood A, in which the parent and fourteen offspring (Plate XL, figs. 1–15) all fall between the figures 50 and 59·5. In other families, although the majority of specimens fall well together there are a few outlying members, but the highest member of any family only comes up to the lower members of the family from the *planemoides* parent (Plate XXXIX). It is impossible to avoid the conclusion that the large size of the spot in the *hippocoön* offspring of *planemoides* is due to the influence upon them of the large size of the corresponding area in the parent, *whose pattern, however, is of quite a different type.*

If the photographs of the three *planemoides* offspring (Plate XXXIX, figs. 4, 6, 8) be compared with *hippocoön* (figs. 2, 3, 5, 7, etc.), an interesting point becomes apparent. Fig. 8, and to a less extent figs. 4 and 6, show in the apical half of the fore-wing a pattern very close to that of *hippocoön*. Fig. 8 in particular exhibits features like those of fig. 9, in which the outer part of the intracellular spot runs out to join the large subapical patch. This latter area in the

photograph of fig. 8 is quite clearly differentiated from the rest of the orange band in the fore-wing, but if one looks at the *specimen* this difference is not so marked. There is therefore some difference in the two parts of the orange band more clearly perceived by the photographic plate than by the human eye. Fig. 8 enables one to realise more clearly how the pattern of the more typical *planemoides* form such as 4 and 6 can influence the *hippocoön* form, and cause the intracellular spot to be of larger size than usual. The pattern of *hippocoön* may be similarly recognised on the under surface of the 3 *planemoides* offspring, where, indeed, the demarcation between the paler orange of the subapical bar of the former pattern is rather more distinctly marked off from the darker orange of the latter than on the upper surface, the junction between the two tints, as it obliquely crosses area 4 (between veins 4 and 5), being faintly emphasised by a slightly deeper shade of the same colour.

Prof. Punnett, F.R.S., in the July number of "Bedrock," 1913, protests "against Prof. Poulton's assumption that any small variation may be inherited," and says "in no clear case has it been shown to exist."

The specimens just mentioned seem to constitute a pretty clear case in which quite a small and relatively unimportant part of the whole pattern of one type derives its unusually large size by heredity from the corresponding area, much larger and less well-defined in shape, of a parent whose pattern is quite different.

Not only is the average size of the spot in the seven specimens under consideration larger than the average of any other brood, but individuals have a larger spot than any of the specimens in the Hope Department from all parts of Africa.

It may be said that it is not fair to compare the *planemoides* family with Mr. Lamborn's families, because W. African specimens have *all* the white areas of the wing contracted in size, thus following their model *Amauris niavius*, L., whose Western form has smaller white areas than the Eastern form *dominicanus*.

An answer to this is provided by the *dardanus* families reared at Durban in Natal by Mr. G. F. Leigh, as well as by the other examples from S.E. Africa; for it will be shown on p. 662 that the average length of the spot in all these *hippocoön* is actually less than that of the

W. African *hippocoön*, although the rest of the pattern is larger. In other words, the spot varies independently of the rest of the pattern.

The Natal families reared by Mr. G. F. Leigh were discussed in great detail by Prof. Poulton in a paper on "Heredity in six families of *P. dardanus*, Brown, subsp. *cenea*, Stoll" (Trans. Ent. Soc., 1908, p. 427), in which the same spot now under discussion was considered, not from the point of view of its size, but as to whether it was divided in two or not. It was shown (*loc. cit.*, p. 444) in one family (No. 5) bred from a *cenea* parent in which this spot was divided, that 9 out of 14 *cenea* offspring also had the spot divided, as also in the only *hippocoön* offspring. Compare this with Family 4 in the same table, and it is seen that the parent *hippocoön* had the spot undivided, and this was also the case in 5 out of 8 *cenea* offspring, 2 out of 3 *hippocoön* offspring, and all of the 3 *trophonius* offspring.

And yet Prof. Punnett says that in no clear case has the inheritance of small variations been shown to exist!

In view of this statement attention may be redirected to sundry papers of Prof. Poulton on this very point as exhibited in the species under discussion. I have shown how the influence of the pattern of a *planemoides* parent is felt by the offspring of the *hippocoön* form as regards *size* of a certain spot. In the Trans. Ent. Soc., 1906, pp. 283, 313, Prof. Poulton shows that the influence of the *colour* of the parent form *trophonius* is felt by offspring of *cenea* form; and again in the Proc. Ent. Soc., 1911, p. xxxvii, he says with regard to another family: "Several of the *cenea* offspring exhibit the influence of the *trophonius* parent in the richer, deeper tinge of the basal patch of the hind-wing."

Again, in Trans. Ent. Soc., 1908, p. 436, he shows how the influence of a parent form *hippocoön* is exhibited in the colour of the *cenea* offspring.

[Since Dr. Carpenter's return to Africa I have observed the following examples of the inheritance of small features that can be made out by a careful comparison between the patterns of the three families represented on Plate XL.—E. B. P.]

(1) Parent D (fig. 16) differs from E (31) in having a larger white area on the hind-wing. This area in its offspring as shown in 17–21 and 30, is larger than in E's

offspring, as shown in 32, 33 and 28. (See also Proc. Ent. Soc., 1912, p. cxxxii.)

(2) The same area is also of a different shape in the two parents, being rounded in E, squarish in D, differences that are clearly recognisable in their respective offspring as shown on Plate XL.

(3) The triangular white patch on the inner margin of the fore-wing is larger, has a more flattened apex, and a longer base in D and its 14 offspring, than in A (fig. 1) and its 14 offspring.

(4) Of the two small spots at the costal end of the sub-apical white bar crossing the fore-wing, the basal one is minute and the outer large in A and most of its offspring, while in none of them is the basal spot as large as the outer. In E on the other hand the basal spot is relatively large and the outer absent: in 6 out of its 7 offspring the basal spot is relatively large as compared with nearly all the offspring of A; while in one (fig. 33) this feature is nearly as in the parent, although the outer spot is represented by a small dot. In the *planemoides* parent (Plate XXXIX, fig. 1) and most of its offspring these two spots are about equal in size, and in only one (fig. 11) is there a wide difference between them.

(5) Other features peculiar to the families, but unrecognisable in the parents, because of their poor condition, are also almost certainly hereditary. To this category belong figs. 10, 12, 13, and 14, in which the white area on the hind-wing is increased by a circumferential greyish extension, giving to the outline a peculiar and characteristic appearance (Proc. Ent. Soc., 1912, pp. xvi, xvii).

Measurement of all the specimens of *hippocoön* in the Hope Department (242) produced interesting results. The West African type is represented by one from Cape Coast Castle, one from "Tropical W. Africa" (Doncaster), 3 from "W. Africa" (Saunders), and 77 (38 shown on Plate XL) caught or bred by Mr. W. A. Lamborn in the vicinity of Lagos. The average ratio of the spot to the cell in these 82 specimens is 64 %—individuals going as low as 44 % and as high as 86 %, with every intermediate grade.

Passing eastward we come to the Western Uganda specimens with which I have included those from a few localities much further east, but always westward of Entebbe:—The "N. W. shore of L. Victoria"—3 specimens;

"Buddu, W. shore of the Lake"—7 specimens; Toro—5 specimens; Unyoro—1 specimen; "neighbourhood of L. Wamala"—1 specimen; the Semliki valley—1 specimen.

These 18 specimens, all collected by Mr. S. A. Neave, seem rather a heterogeneous lot, but the average size of the spot is practically the same as in the West Coast forms, viz. 65·2 %. Individuals range between 39·7 % and 86·9 %.

From the northern shore of the lake in the neighbourhood of Entebbe, from the islands, and from the neighbourhood of Kisumu on the Eastern shore come altogether 85 specimens. From Entebbe Mr. C. A. Wiggins sent 55 specimens, and Mr. Sheffield Neave contributed 8, and 5 more from Kampala. There is a single specimen from the Mabira forest (Wiggins) and 8,—seven of them represented on Plate XXXIX—from Bugalla Island (G. D. H. Carpenter).

From the neighbourhood of Kisumu on the E. shore of the lake come 7 specimens contributed by C. A. Wiggins and one by A. Vincent. These specimens are included with those from Entebbe rather than with the other specimens from E. Africa which are of the subspecies *tibullus*, Kirby, and come from localities far removed from the E. shore of the lake.

The average for these 85 specimens is not far from the West Coast average: but there is a greater range of variation, viz. from 38 % to 102 % (Plate XXXIX, fig. 9). Passing eastwards we come now to the locality of the subspecies *tibullus*, Kirby, and *polytrophus*, Jordan. These are represented by 11 *hippocoön* caught by K. St. A. Rogers near Mombasa, 2 by the same collector on the slopes of Kilimanjaro, 1 from Taveta by C. A. Wiggins, 4 from Kikuyu Escarpment by W. Doherty (these latter belong to the subspecies *polytrophus*), and a single specimen (Doncaster) from German East Africa. I have also included in this group, perhaps unjustifiably, a single specimen collected by S. A. Neave in Eastern Usoga, in the far E. of Uganda, whose spot-cell ratio was 78·2 %. The average figure for these 20 specimens is 78 %, and they are a fairly uniform lot, all coming between 71·4 % and 90·5 %, with the exception of one at 62·5 %.

There is another fine series of the subspecies *tibullus* collected by C. F. M. Swynnerton at Chirinda, Gazaland, S.E. Rhodesia. These 21 specimens have an average spot-cell ratio of 80 %, and are also a very compact group, ranging from 70·4 % to 91·2 %.

Finally the *hippocoön* form of the Southern race of *dardanus* is represented in the Hope Department by 12 specimens from the neighbourhood of Durban caught or bred by G. F. Leigh; one from Malvern, Natal, by G. A. K. Marshall; one from Cape Colony near King Williamstown, by J. P. M. Weale.

It must be remembered that the *hippocoön* of the S.E. coast has the main white areas on fore- and hind-wings *larger* than in the West Coast forms, corresponding to the *dominicanus*, Trim., form of its model *Amauris niavius* in E. Africa. Unfortunately, owing to the mixed character of the offspring from a parent in Durban, the number of *hippocoön* females in any family is small. The figures are as follows: From a *hippocoön* parent, whose spot-cell ratio was 68·3 %, there were three *hippocoön* forms, the figures for which were 60 %, 56·7 %, 47·2 %. From a *trophonius*, Westw., parent there were only two *hippocoön* offspring, whose figures were 52·9 % and 54·5 %. From a *cenea*, Stoll, parent two *hippocoön* offspring, 58·6 % and 64·5 %.

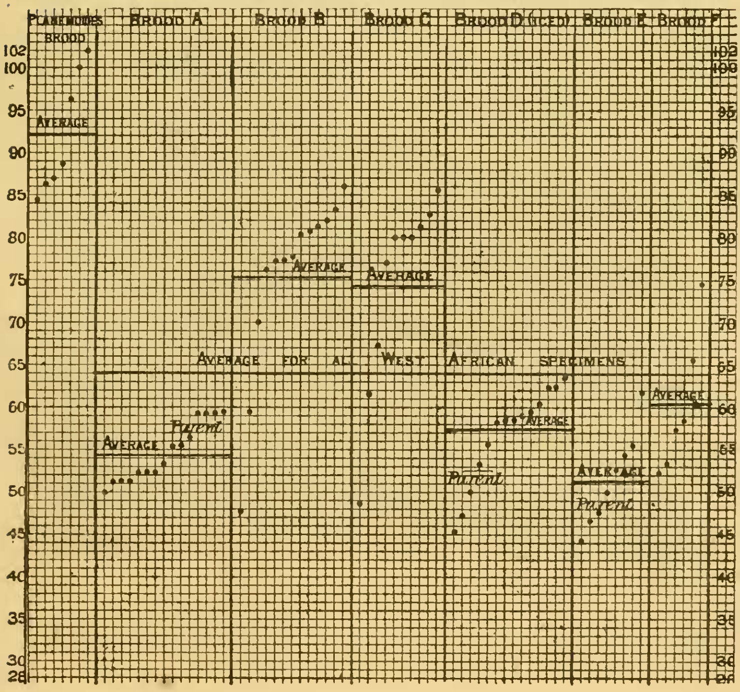
Since writing the above I have had an opportunity, through the kindness of Mr. Roland Trimen, F.R.S., of measuring the spot in five specimens in his private collection —3 from Natal and 2 from Cape Colony. These 19 Southern specimens range from 47·2 % to 77·5 %, with an average ratio of spot to cell of 61·2 %. It will be seen that the comparison of the average size of the West African spot with that of the Southern and Eastern form suggests a point of considerable importance to the argument developed in this paper. The *hippocoön* of Natal, which mimics *Amauris niavius dominicanus*, has the important white areas of the wings *larger* than in the *hippocoön* of the West Coast, mimicking *Amauris niavius* in which the white areas are also smaller than in the Eastern model. But the intracellular white spot, which is not of so much importance for the mimetic likeness, is, on the *average*, actually *smaller* in the Natal and Cape Colony forms than in the West Coast forms.

The above-described relationship disposes of an argument which might be stated against the conclusion here drawn (that the large size of the spot in *hippocoön* derived from *planemoides* is due to the hereditary influence of this small feature), namely the objection that the size of the spot in the *hippocoön* offspring is not due to a separate factor,

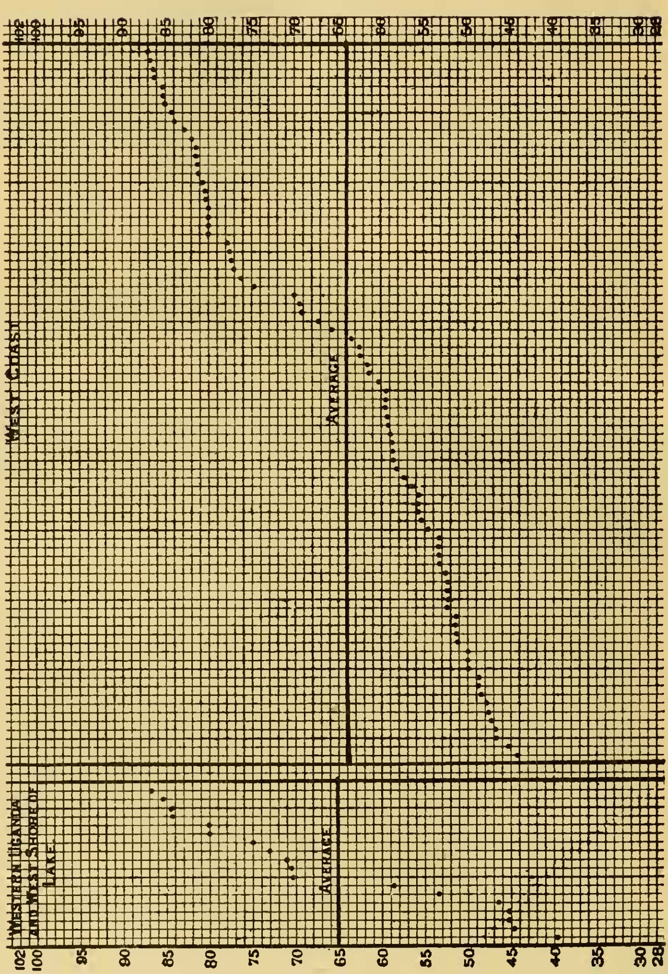
but simply part of the general scheme of enlarged white areas in the Southern and Eastern form as compared with the Western.

But the spot is, on the average, actually smaller in the Natal forms than in the Western forms, whereas the reverse in the case with the large white areas which are of most importance for the mimetic resemblance. Furthermore the 7 *hippocoön* offspring of the female *planemoides*, like the other examples of *hippocoön* from Uganda, belong to the Western and not to the Eastern type; and yet the spots of these 7 specimens are the largest of all.

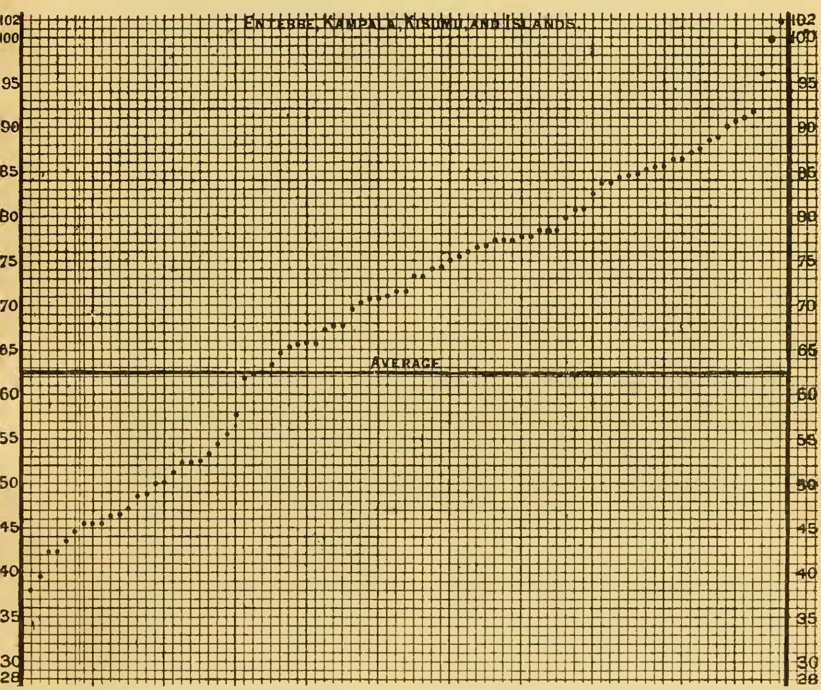
SPOT-CELL-RATIO IN *HIPPOCOÖN* OFFSPRING FROM A *PLANEMOIDES* PARENT (BUGALLA ISLAND) AND FROM SIX *HIPPOCOÖN* PARENTS (LAGOS DISTRICT).



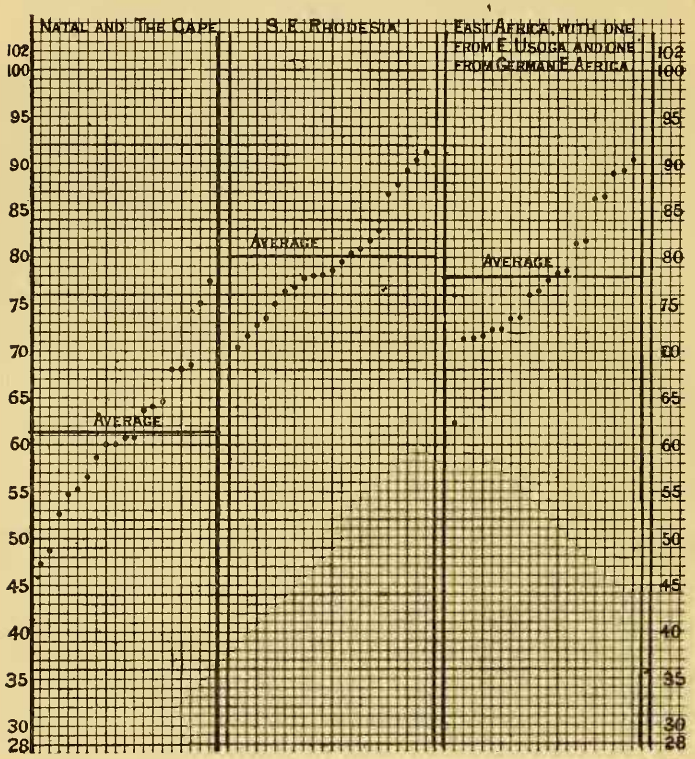
Spot-cell-ratio in *Hippocoön* from West Coast, W. Uganda, and W. shore of Victoria Nyanza.



SPOT-CELL-RATIO IN *HIPPOCOÖN* FROM ENTEBBE, KAMPALA, ISLANDS IN N.W. VICTORIA NYANZA, AND KISUMU.



Spot-cell-ratio in *hippocoön* from East Africa, S. E. Rhodesia, and S. Africa.



Explanation of Plates XXXIX and XL.

[*See Explanations facing the* Plates.]